Chapter 39

Plant Responses to Internal and External Signals

Lecture Outline

Overview: Stimuli and a Stationary Life

- Some plants open and close their flowers at the particular times of the day when their insect pollinators are most active.
- The passage of time is only one of many environmental factors that a plant must sense in order to survive and reproduce successfully.
- At the organismal level, plants and animals respond to environmental stimuli by very different means.
  - Animals, being mobile, respond mainly by behavioral mechanisms, moving toward positive stimuli and away from negative stimuli.
  - Plants are stationary and generally respond to environmental cues by adjusting their patterns of growth and development.
  - As a result, plants of the same species vary in body form much more than do animals.
- Before plants can initiate growth responses to environmental signals, they must detect the change in their environment.
- At the cellular level, the processes by which plants and animals perceive environmental changes are equally complex and often homologous.

Concept 39.1 Signal transduction pathways link signal reception to response

- Plants receive specific environmental signals and respond to them in ways that enhance their survival and reproductive success.
- A potato (a modified underground stem) kept in the dark sprouts shoots from its "eyes" (axillary buds).
  - These shoots are ghostly pale and have long, thin stems, unexpanded leaves, and reduced roots.
- These morphological adaptations for growing in darkness, called **etiolation**, also occur in seedlings germinated in the dark and make sense for plants that sprout underground.
  - Expanded leaves would hinder soil penetration and be damaged as the shoot pushes upward.
  - Because little water is lost in transpiration, an extensive root system is not required.
  - The production of chlorophyll is unnecessary in the absence of light.
  - A plant growing in the dark allocates as much energy as possible to the elongation of stems in order to break ground before the nutrient reserves in the tuber are exhausted.

- Once a shoot reaches the sunlight, its morphology and biochemistry undergo profound changes, collectively called **de-etiolation** or greening.
    - The elongation rate of the stems slows, the leaves expand, the roots start to elongate, and the shoot produces chlorophyll.
- The de-etiolation response is an example of how a plant receives a signal—in this case, light—and how this reception is transduced into a response (greening).
- Studies of mutants have provided valuable insights into the roles that various molecules play in the three stages of cell-signal processing: reception, transduction, and response.
- Signals are first detected by receptors, proteins that change shape in response to a specific stimulus.
- The receptor for de-etiolation in plants is called a *phytochrome.*
    - Unlike most receptors, which are in the plasma membrane, this type of phytochrome is in the cytoplasm.
- The importance of phytochrome was confirmed through investigations of a tomato mutant called *aurea*, which greens less than wild-type tomatoes when exposed to light.
    - Injecting additional phytochrome from other plants into *aurea* leaf cells and exposing them to light produced a normal de-etiolation response, indicating that phytochrome functions in light detection during de-etiolation.
- Receptors such as phytochrome are sensitive to very weak environmental and chemical signals.
    - A de-etiolation response may be triggered by exposure to a few seconds of moonlight.
- Weak signals are amplified by **second messengers**—small molecules and ions that amplify the signal and transfer it from the receptor to proteins that cause the response.
- Light causes phytochrome to undergo a conformational change that leads to increases in the levels of two second messengers: cyclic GMP (cGMP) and Ca^{2+}.
- Changes in cytosolic Ca^{2+} levels play an important role in phytochrome signal transduction.
    - The concentration of Ca^{2+} is generally very low in the cytosol (about 10^{-7} *M*).
    - Phytochrome activation opens Ca^{2+} channels and leads to transient 100-fold increases in cytosolic Ca^{2+}.
- In response to light, phytochrome undergoes a change in shape that leads to the activation of guanylyl cyclase, an enzyme that produces the second messenger cyclic GMP.
- Both Ca^{2+} and cGMP must be produced for a complete de-etiolation response.
    - Injection of cGMP into *aurea* tomato leaf cells induces only a partial de-etiolation response.
- Ultimately, second messengers regulate one or more cellular activities.
    - These responses involve the increased activity of certain enzymes through two mechanisms: by post-translational modification (activating existing enzymes) or by transcriptional regulation (modifying synthesis of specific mRNA molecules).

Pre-existing proteins may undergo post-translational modification.

- In signal transduction pathways, pre-existing proteins are modified by the phosphorylation of specific amino acids, which alters the protein's hydrophobicity and activity.
    - Many second messengers, including cGMP and Ca^{2+}, activate protein kinases directly.

- Often, one protein kinase will phosphorylate another protein kinase, which then phosphorylates another.
- Such kinase cascades link initial stimuli to responses at the level of gene expression via phosphorylation of transcription factors.

- Many signal transduction pathways ultimately regulate the synthesis of new proteins by turning specific genes on or off.
- Signal transduction pathways can also turn off when the initial signal is no longer present.
    - Protein phosphatases that dephosphorylate specific protein, are important in these "switch-off" processes.
- At any moment, a cell's activities depend on the balance of activity of many types of protein kinases and protein phosphatases.

Transcriptional regulation is also important.

- In transcriptional regulation, *specific transcription factors* bind to specific regions of DNA and control the transcription of specific genes.
- In the case of phytochrome-induced de-etiolation, several transcription factors are activated by phosphorylation in response to the appropriate light conditions.
    - Activation of some of these transcription factors depends on their phosphorylation by protein kinases activated by cGMP or Ca^{2+}.
- The mechanism by which a signal promotes a new course of development may depend on transcription factors that are activators (*increasing* transcription of specific genes) or repressors (*decreasing* transcription).
- Some *Arabidopsis* mutants have a light-grown morphology (expanded leaves and short, sturdy stems) when grown in the dark.
    - They are not green because the final step in chlorophyll production requires light.
    - The mutants have defects in a repressor that inhibits the expression of other genes normally activated by light.
    - When the repressor is eliminated by mutation, the blocked pathway becomes activated.
    - Hence, these mutants, except for their pale color, appear to have been grown in the light.
- During the de-etiolation response, a variety of proteins are either synthesized or activated.
    - These proteins include enzymes that function in photosynthesis directly, others that supply chemical precursors for chlorophyll production, and some that affect the levels of plant hormones that regulate growth.
    - For example, the levels of two hormones (auxins and brassinosteroids) that enhance stem elongation decrease following phytochrome activation, reducing the stem elongation that accompanies de-etiolation.

Concept 39.2 Plant hormones help coordinate growth, development, and responses to stimuli

- **Hormones** are signaling molecules produced in tiny amounts in one part of the body and transported to other parts of the body, where they bind to specific receptors and trigger responses in target cells and tissues.
    - In animals, hormones are usually transported through the circulatory system.

- Plants and animals differ in their responses to hormones.
  - Plants lack blood or a circulatory system to transport hormone-like signal molecules.
  - Some plant hormones act only locally.
- Some signal molecules in plants, such as sucrose, typically occur at concentrations that are hundreds of thousands times higher than the concentration of a typical hormone.
  - Nevertheless, these signal molecules are transported through plants and activate signal transduction pathways that greatly alter the functioning of plants.
- Many researchers prefer the broader term *plant growth regulator* for natural or synthetic organic compounds that modify or control specific physiological processes within a plant.
  - For historical continuity, we will use the term *plant hormone* and adhere to the criterion that plant hormones are active at very low concentrations.
- Virtually every aspect of plant growth and development is under hormonal control to some degree.
- A single hormone can regulate a diverse array of cellular and developmental processes.
  - Conversely, multiple hormones may influence a single process.

Research on how plants grow toward light led to the discovery of plant hormones.

- Plants grow toward light.
- Any growth response that results in curvature of whole plant organs toward or away from stimuli is called a **tropism**.
  - The growth of a shoot toward light is called positive **phototropism**; growth away from light is negative phototropism.
- In natural ecosystems, positive phototropism directs shoot growth toward the sunlight that powers photosynthesis.
  - This response results from a differential growth of cells on opposite sides of the shoot: The cells on the darker side elongate faster than the cells on the brighter side.
- In the late 1800s, Charles Darwin and his son Francis observed that a grass seedling within a coleoptile bent toward light only if the tip of the coleoptile was present.
  - This response stopped if the tip was removed or covered with an opaque cap (but not a transparent cap or an opaque shield below the coleoptile tip).
  - The Darwins concluded that the tip of the coleoptile was able to sense light.
- The differential growth response occurred some distance below the tip, leading the Darwins to postulate that some signal was transmitted from the tip downward.
- A few decades later, Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance.
  - He separated the tip from the remainder of the coleoptile by a block of gelatin, thus preventing cellular contact but allowing chemicals to pass.
  - These seedlings responded normally, bending toward light.
  - If the tip was separated from the lower coleoptile by an impermeable barrier such as mica, no phototropic response occurred.
- In 1926, Frits Went extracted the chemical messenger for phototropism, naming it *auxin.*
  - Went placed excised coleoptile tips on agar blocks and collected the substance that diffused into the agar.

- If an agar block with this substance was centered on a coleoptile without a tip, the plant grew straight upward.
- If the block was placed on one side, the plant bent away from the agar block.

- Went concluded that the agar block contained a chemical produced in the coleoptile tip, that this chemical stimulated growth as it passed down the coleoptile, and that a coleoptile curved toward light because of a higher concentration of the growth-promoting chemical on the darker side of the coleoptile.
- The major type of auxin was later purified and identified as indoleacetic acid (IAA).
- The classical hypothesis for what causes grass coleoptiles to grow toward light, based on these experiments, is that an asymmetrical distribution of auxin moving down from the coleoptile tip causes cells on the darker side to elongate faster than cells on the brighter side.
- However, studies of phototropism by organs other than grass coleoptiles provide little support for this idea.
    - There is no evidence that illumination from one side causes an asymmetrical distribution of auxin in the stems of sunflowers or other eudicots.
    - There *is* an asymmetrical distribution of certain substances that may act as growth *inhibitors*, with these substances more concentrated on the lighter side of a stem.

Plant hormones help coordinate growth, development, and responses to environmental stimuli.

- Some of the major classes of plant hormones are auxins, cytokinins, gibberellins, brassinosteroids, abscisic acid, strigolactones, and ethylene.
    - Many molecules that function in plant defenses against pathogens are probably plant hormones as well.
- Plant hormones are produced at very low concentrations.
- Signal transduction pathways amplify the hormonal signal many-fold and connect it to a cell's specific responses.
- In general, plant hormones control plant growth and development by affecting the division, elongation, and differentiation of cells.
- Some hormones also mediate shorter-term physiological responses of plants to environmental stimuli.
- Each hormone has multiple effects, depending on its site of action, its concentration, and the developmental stage of the plant.
- Response to a hormone usually depends not so much on its absolute concentration as on its relative concentration compared to other hormones.
- It is hormonal balance, rather than hormones acting in isolation, that controls growth and development of plants.

Auxins have multiple functions in flowering plants.

- The term **auxin** is used for any chemical substance that promotes the elongation of coleoptiles, although auxins actually have multiple functions in angiosperms.
- The major natural auxin occurring in plants is indoleacetic acid (IAA), but several other compounds also have auxin activity.
- Auxin is produced in shoot tips and transported cell-to-cell down the stem at a rate of about 1 cm/hr.

- In the shoot, auxin moves from tip to base. This unidirectional transport of auxin is called *polar transport* and has nothing to do with gravity.
  - Auxin travels upward if a stem or coleoptile is placed upside down.
- The polarity of auxin transport is due to the polar distribution of auxin transport protein in the cells.
  - Concentrated at the basal end of the cells, auxin transporters move the hormone out of the cell and into the apical end of the neighboring cell.
- One of auxins chief functions is to stimulate the elongation of cells in young shoots.
- As auxin moves from the apex down to the region of cell elongation, the hormone stimulates cell growth by binding to a receptor in the plasma membrane.
  - Auxin stimulates cell growth over only a certain concentration range—from about 10^{-8} to 10^{-4} *M*.
  - At higher concentrations, auxins may inhibit cell elongation, probably by inducing the production of ethylene, a hormone that generally hinders growth.
- According to the *acid growth hypothesis*, in a shoot's region of elongation, auxin stimulates the plasma membrane's proton (H^+) pumps, increasing the membrane potential and lowering the pH in the cell wall.
  - Lowering the pH activates **expansin** enzymes that break the cross-links between cellulose microfibrils and other cell wall constituents, loosening the wall.
  - Increasing the membrane potential enhances ion uptake into the cell, which causes the osmotic uptake of water and increase turgor, allowing the cell to elongate.
- Auxin rapidly alters gene expression, causing cells in the region of elongation to produce new proteins within minutes.
  - Some of these proteins are short-lived transcription factors that repress or activate the expression of other genes.
- Auxin stimulates a sustained growth response of making the additional cytoplasm and wall material required by elongation.

Auxin plays a role in plant development.

- Auxin plays a role in almost all aspects of plant spatial organization or *pattern formation*.
- Since auxin is formed by shoot tips, it carries integrated information about the development, size, and environment of individual branches.
- This flow of information controls branching patterns.
  - A reduced flow of auxin from a branchindicates that the branch is not being sufficiently productive: New branches are needed elsewhere.
  - Lateral buds below the branch are released from dormancy and begin to grow.
- Auxin transport also plays a key role in establishing *phyllotaxy*, the arrangement of leaves on the stem.
  - Polar auxin transport in the plant apex generates local peaks in auxin concentration that determine the site of leaf primordia formation.
- Polar transport of auxin from the leaf margin also directs leaf venation patterns.
  - Inhibitors of polar auxin transport result in leaves that lack vascular continuity through the petiole and have broad, loosely organized main veins, an increased number of

secondary veins, and a dense band of irregularly shaped vascular cells adjacent to the leaf margin.

- The activity of the vascular cambium that produces woody tissues is under the control of auxin transport.
  - When a plant becomes dormant at the end of a growing season, auxin transport capacity and the expression of genes encoding auxin transporters are reduced.

Auxins have many practical uses.

- Natural and synthetic auxins have many commercial applications.
- The natural auxin indolebutyric acid (IBA) is used in the vegetative propagation of plants by cuttings.
  - Treating a detached leaf or stem with powder containing IBA causes adventitious roots to form near the cut surface.
- Synthetic auxins such 2,4-dichlorophenoxyacetic acid (2,4-D) are widely used as herbicides.
  - Monocots, such as maize or turfgrass, can rapidly inactivate these synthetic auxins.
  - Dicots cannot activate the synthetic auxins and die from a hormonal overdose.
  - Spraying cereal fields or turf with 2,4-D kills dicot (broadleaf) weeds such as dandelions.
- Developing seeds synthesize auxin, which promotes fruit growth.
  - Synthetic auxins sprayed on tomato vines induce the development of seedless tomatoes without pollination.

Cytokinins stimulate cytokinesis.

- In the 1940s, researchers stimulated the growth of cultured plant embryos by adding coconut milk, the liquid endosperm of a coconut seed.
- Cultured tobacco cells can be induced to divide by adding degraded samples of DNA.
  - The active ingredients in both cases were modified forms of adenine.
- These growth regulators were named **cytokinins** because they stimulate cytokinesis, or cell division.
- Much remains to be learned about cytokinin synthesis and signal transduction, but the effects of cytokinins on cell division and differentiation, apical dominance, and aging are well known.
- Cytokinins are produced in actively growing tissues, especially roots, embryos, and fruits.
  - Cytokinins produced in roots reach their target tissues by moving up the plant in the xylem sap.
- Cytokinins interact with auxins to stimulate cell division and influence differentiation.
  - If parenchyma tissue is grown in tissue culture without cytokinins, the cells grow large but do not divide.
  - If cytokinins and auxins are added, the cells divide.
  - Cytokinins alone have no effect.
- The ratio of cytokinins to auxins controls cell differentiation.
  - If the ratio of cytokinins to auxins is at a particular level, then the mass of growing cells, called a callus, remains undifferentiated.
  - If cytokinin levels are raised, shoot buds develop from the callus.
  - If auxin levels are raised, roots form.

- Cytokinins, auxins, and a newly discovered plant hormone called strigolactone interact in the control of apical dominance, the ability of the apical bud to suppress the development of axillary buds.
- Until recently, the leading hypothesis for the role of hormones in apical dominance—the direct inhibition hypothesis—proposed that auxins and cytokinins act antagonistically in regulating axillary bud growth.
  - In this hypothesis, Auxins transported down the shoot from the apical bud inhibit axillary bud growth, causing the shoot to lengthen without branching.
  - Cytokinins entering the shoot system from the roots signal axillary buds to grow.
- Many observations are consistent with the direct inhibition hypothesis.
  - If the apical bud, the primary source of auxins, is removed, the inhibition of axillary buds is removed and the plant becomes bushier.
  - This action can be inhibited by adding auxins to the cut surface.
  - Mutants that overproduce cytokinins or plants treated with cytokinins are bushy.
- In fact, auxin's effects are partially indirect.
  - Polar flow of auxin down the shoot triggers the synthesis of strigolactone, which represses bud growth.
  - Another signal, perhaps an electrical one, causes buds to begin growing much earlier than can be explained by disrupted auxin flow.
- Cytokinins slow the aging of some plant organs by inhibiting protein breakdown, stimulating RNA and protein synthesis, and mobilizing nutrients from surrounding tissues.
  - Leaves removed from a plant and dipped in a cytokinin solution stay green longer.
  - Cytokinins also slow the progress of programmed cell death in intact plants.

Gibberellins have a variety of effects, including stem elongation, fruit growth, and seed germination.

- In early 1900s, farmers in Asia noticed that some rice seedlings grew so tall and spindly that they toppled over before they could mature and flower.
- In 1926, a fungus in the genus *Gibberella* was found to cause this "foolish seedling disease."
- The fungus caused hyperelongation of rice stems by secreting a chemical called **gibberellin**.
- In the 1950s, researchers discovered that plants also make gibberellins (GAs).
- Researchers have identified more than 100 different natural gibberellins.
  - Typically each plant produces a much smaller number.
  - "Foolish rice" seedlings suffer from too much gibbberellin.
- Young roots and leaves are the major sites of gibberellin production.
- Gibberellins stimulate stem and leaf growth by increasing cell elongation *and* cell division.
  - One hypothesis proposes that gibberellins stimulate cell wall–loosening enzymes, facilitating the entry of expansin proteins.
  - In a growing stem, auxins and gibberellins act in concert to promote elongation.
- The effects of gibberellins in enhancing stem elongation are evident when dwarf varieties of plants are treated with gibberellins.
  - After treatment with gibberellins, some dwarf pea plants grow to normal height.

- If gibberellins are applied to wild-type plants, there is often no response because these plants are already producing an optimal dose of the hormone.

- The most dramatic example of gibberellin-induced stem elongation is *bolting*, the rapid formation of the floral stalk.
- In many plants, both auxin and gibberellins must be present for fruit to set.
- If Thompson seedless grapes are sprayed with gibberellin during development, the internodes of the grape bunch elongate, allowing more space for each grape.
  - The extra space promotes air circulation between the grapes and makes it harder for yeast and other microorganisms to infect the fruits.
- The embryo of a seed is a rich source of gibberellins.
  - After water is imbibed, the release of gibberellins from the embryo signals the seed to break dormancy and germinate.
  - Some seeds that require special environmental conditions to germinate, such as exposure to light or low temperatures, break dormancy when they are treated with gibberellins.
  - Gibberellins support the growth of cereal seedlings by stimulating the synthesis of digestive enzymes that mobilize stored nutrients.

Brassinosteroids have effects similar to those of auxin.

- **Brassinosteroids** are steroids similar to cholesterol and the sex hormones of animals.
- Brassinosteroids induce cell elongation and division in stem segments and seedlings at concentrations as low as 10^{-12} M.
- They also slow leaf abscission and promote xylem differentiation.
- Their effects are so qualitatively similar to those of auxins that it took several years for plant physiologists to recognize that brassinosteroids were not types of auxins.
- Identification of brassinosteroids arose from studies of an *Arabidopsis* mutant with morphological features similar to those of light-grown plants even when grown in the dark.
  - The mutation affects a gene that normally codes for an enzyme similar to one involved in steroid synthesis in mammalian cells.
  - The mutant was restored to normal by the experimental application of brassinosteroids.

Abscisic acid slows growth.

- **Abscisic acid (ABA)** was discovered in the 1960s, when one research group studying bud dormancy and another investigating leaf abscission isolated ABA.
- ABA is an important plant hormone with a variety of functions.
- ABA generally *slows* growth by antagonizing the actions of the growth hormones—auxins, cytokinins, gibberellins, and brassinosteroids.
  - The ratio of ABA to one or more growth hormones determines the final physiological outcome.
- One major effect of ABA on plants is seed dormancy.
  - Seed dormancy has great survival value because it ensures that seeds germinate only when there are optimal conditions of light, temperature, and moisture.
- Levels of ABA may increase 100-fold during seed maturation, inhibiting germination and inducing the production of special proteins that help seeds withstand the extreme dehydration that accompanies maturation.

- Many types of dormant seeds germinate when ABA is removed or inactivated.
  - The seeds of some desert plants break dormancy only when heavy rains wash out ABA.
  - Other seeds require light or prolonged exposure to cold to inactivate ABA.
- The ratio of ABA to gibberellins determines whether the seed remains dormant or germinates.
  - The addition of ABA to seeds that are about to germinate makes them dormant again.
  - Inactivated ABA or low levels of ABA can lead to early germination.
  - A maize mutant whose seeds germinate while still on the cob lacks a functional transcription factor required for ABA to induce expression of certain genes.
- ABA plays a major role in drought signaling.
  - When a plant begins to wilt, ABA accumulates in leaves and causes stomata to close rapidly, reducing transpiration and preventing further water loss.
  - ABA causes an increase in the opening of potassium channels in the plasma membrane of guard cells, leading to a massive loss of potassium from the cells.
  - The accompanying osmotic loss of water leads to a reduction in guard cell turgor, and the stomatal pores close.
  - In some cases, water shortages can stress the root system early, leading to the transport of ABA from roots to leaves and functioning as an "early warning system."
  - Mutants that are prone to wilting are often deficient in ABA production.

Strigolactones stimulate seed germination, promote mycorrhizal associations, and control apical dominance.

- The recently discovered Strigolactones are named for *Striga,* a genus of rootless parasitic plants that penetrate the roots of other plants, diverting essential nutrients from them and stunting their growth.
- *Striga* may be the greatest obstacle to food production in Africa, infesting about two-thirds of the area devoted to cereal crops.
  - Each *Striga* plant produces tens of thousands of tiny seeds that remain dormant in the soil for many years until a suitable host is available.
- Strigolactones exuded by the host roots were first identified as the chemical signals that stimulate the germination of *Striga* seeds.

The gas ethylene is a plant hormone.

- In 1901, it was demonstrated that the gas **ethylene** was the active factor that caused leaves to drop prematurely from trees near leaking gas mains.
- Plants produce ethylene in response to stresses such as drought, flooding, mechanical pressure, injury, and infection.
- Ethylene production also occurs during fruit ripening, during programmed cell death, and in response to high concentrations of externally applied auxins.
- Ethylene instigates a seedling to perform a growth maneuver called the **triple response** that allows a seedling to circumvent an obstacle such as a stone as it grows through soil.
- In the triple response, stem elongation slows, the stem thickens, and curvature causes the stem to start growing horizontally.
- As the effects of the initial ethylene pulse lessen, the stem resumes vertical growth.

- If the stem again detects a rock, another pulse of ethylene is generated, and the stem continues its horizontal progress.
- If upward touch detects no solid object, ethylene production decreases, and the stem resumes normal upward growth.

- It is ethylene, not the physical obstruction, which induces the stem to grow horizontally.
    - Normal seedlings that grow free of all physical impediments undergo the triple response if ethylene is applied.
- *Arabidopsis* mutants with abnormal triple responses have been used to investigate the signal transduction pathways leading to this response.
- Ethylene-insensitive *(ein)* mutants may fail to undergo the triple response after exposure to ethylene because they lack a functional ethylene receptor.
- Ethylene-overproducing *(eto)* mutants undergo the triple response in the absence of physical obstacles because they produce ethylene at 20 times the normal rate.
    - They can be restored to wild type by treatment with inhibitors of ethylene synthesis.
- Other mutants, called constitutive triple-response *(ctr)* mutants, undergo the triple response in air but do not respond to inhibitors of ethylene synthesis.
    - Ethylene signal transduction is permanently turned on, even when no ethylene is present.
- Constitutive triple-response (*ctr*) mutants undergo the triple response in air but do not respond to inhibitors of ethylene synthesis.
    - In *ctr mutants*, ethylene signal transduction is permanently turned on, even though ethylene is not present.
- The affected gene in *ctr* mutants codes for a protein kinase.
    - This mutation *activates* the ethylene response, suggesting that the normal kinase product of the wild-type allele is a *negative* regulator of ethylene signal transduction.
- Binding of the hormone ethylene to a receptor normally leads to inactivation of the kinase.
    - Inactivation of this negative regulator allows synthesis of the proteins required for the triple response.
- **Senescence** is the programmed death of certain cells or organs or the entire plant.
- Cells, organs, and plants that are genetically programmed to die on schedule do not simply shut down their cellular machinery and await death.
- During programmed cell death, or **apoptosis**, there is active expression of new genes that produce enzymes that break down many chemical components, including chlorophyll, DNA, RNA, proteins, and membrane lipids.
- A burst of ethylene production is associated with apoptosis.
- The loss of leaves each autumn is an adaptation that protects deciduous trees from desiccation during winter, when their roots cannot absorb water from the frozen ground.
- Before leaves abscise, many essential elements are salvaged from the dying leaves and stored in stem parenchyma cells.
    - These nutrients are recycled back to developing leaves the following spring.
- When a leaf falls in autumn, the breaking point is an abscission layer at the petiole base.
- These parenchyma cells have very thin walls and lack fiber cells around the vascular tissue.

- The abscission layer is further weakened when enzymes hydrolyze polysaccharides in the cell walls.
- The weight of the leaf, with the help of the wind, causes a separation within the abscission layer.
- Before the leaf falls, a layer of cork forms a protective scar on the twig side of the abscission layer, preventing pathogens from invading the plant.

- A change in the balance of ethylene and auxin controls abscission.
  - An aging leaf produces less auxin, increasing the sensitivity of abscission layer cells to ethylene.
  - Under the influence of ethylene, cells in the abscission layer produce enzymes that digest the cellulose and other components of cell walls.
- Fruit ripening is triggered by a burst of ethylene production.
  - Enzymatic breakdown of cell wall components softens the fruit, and the conversion of starches and acids to sugars makes the fruit sweet.
  - The production of new scents and colors helps advertise fruits' ripeness to animals, which eat the fruits and disperse the seeds.
  - A chain reaction occurs during ripening: Ethylene triggers ripening, and ripening triggers more ethylene production.
- Molecular biologists have blocked the transcription of a gene required for ethylene synthesis in tomato plants.
  - These tomato fruits are picked while green and are induced to ripen on demand by the addition of ethylene gas.
- Plant responses may involve the interactions of many hormones and their signal transduction pathways.
- Many plant biologists promote a systems-based approach, which attempts to discover and understand biological properties emerging from the interactions of many system elements.
- Using genomic techniques, biologists can identify all the genes in a plant.
  - Many plants have been sequenced, including *Arabidopsis,* rice, grape, maize, and poplar.
- Using microassay and proteomic techniques, scientists can determine which genes are inactivated or activated in response to an environmental change.
- A systems-based approach may greatly alter how plant biology is done.
  - Laboratories equipped with fast-moving (high-throughput) robotic scanners will record which genes in a plant's genome are activated in which cells and under what conditions.
  - New hypotheses and avenues of research will emerge from analysis of these comprehensive data sets.
- One goal of systems biology is to model a living plant and predict the results of genetic manipulation.

Concept 39.3 Responses to light are critical for plant success

- Light is an important environmental factor in the lives of plants.
- Light is required for photosynthesis and cues key events in plant growth and development.

- The effects of light on plant morphology are called **photomorphogenesis**.
- Light reception allows plants to measure the passage of days and seasons.
- Plants detect the presence, direction, intensity, and wavelength of light.
- A graph called an **action spectrum** depicts the relative effectiveness of different wavelengths of radiation in driving a particular process.
- Action spectra can be useful in the study of *any* process that depends on light.
  - A close correspondence between the action spectrum of a plant response and the absorption spectrum of a purified pigment suggests that the pigment may be the photoreceptor involved in mediating the response.
- Action spectra reveal that red and blue light are the most important in regulating a plant's photomorphogenesis.
- Researchers identified two major classes of light receptors: **blue-light photoreceptors** and **phytochromes** that absorb mostly red light.
- The action spectra of many plant processes demonstrate that blue light is effective in initiating diverse responses.
- The biochemical identity of the blue-light photoreceptor was so elusive that it was called cryptochrome.
- In the 1990s, molecular biologists analyzing *Arabidopsis* mutants found three completely different types of pigments that detect blue light.
  - *Cryptochromes* are molecular relatives of DNA repair enzymes, involved in the inhibition of stem elongation.
  - *Phototropin* is a protein kinase involved in mediating phototropic curvature and chloroplast movements in response to light.
  - There is debate about whether phototropin or a carotenoid-based photoreceptor called *zeaxanthin* is the major blue-light photoreceptor involved in stomatal opening.

Phytochromes regulate many plant responses to light.

- Phytochromes were discovered in studies of seed germination.
- Because of limited food resources, small seeds, such as lettuce, sprout successfully only when they germinate under near-optimal conditions, especially light conditions.
  - Such seeds often remain dormant for many years until light conditions change and the death of a shading tree or the plowing of a field creates a favorable light environment.
- In the 1930s, scientists at the U.S. Department of Agriculture determined the action spectrum for light-induced germination of lettuce seeds.
- The scientists exposed water-swollen seeds to a few minutes of monochromatic light of various wavelengths, stored the seeds in the dark for two days, and then recorded the number of seeds that had germinated under each light regimen.
  - Red light (660 nm) increased germination, but far-red light (730 nm) *inhibited* it.
  - The response depends on the *last* flash of light; the effects of red and far-red light are reversible.
- The photoreceptor responsible for these opposing effects of red and far-red light is a phytochrome.

- A phytochrome consists of two identical subunits, each consisting of a polypeptide covalently bonded to a *chromophore*, the light-absorbing part of the molecule.
  - Researchers have identified five phytochromes in *Arabidopsis,* each with a slightly different polypeptide component.
- The chromophore of a phytochrome is photoreversible and reverts back and forth between two isomeric forms.
  - P_r absorbs red light (r) maximally and converts to P_{fr}.
  - P_{fr} absorbs far-red light (fr) maximally and converts to P_r.
- This interconversion between isomers is a switching mechanism that controls various light-induced events in the life of the plant.
- The P_{fr} form triggers many of the plant's developmental responses to light.
  - P_r in lettuce exposed to red light is converted to P_{fr}, stimulating cellular responses that lead to germination.
- Plants synthesize phytochrome as P_r, and if seeds are kept in the dark, the pigment remains almost entirely in the P_r form.
- If the seeds are illuminated with sunlight, the phytochrome is exposed to red light (along with other wavelengths), and much of the P_r is converted to P_{fr}, triggering germination.
- The phytochrome system also provides plants with information about the *quality* of light.
- During the day, sunlight includes both red and far-red radiation, and the $P_r \leftrightarrow P_{fr}$ photoreversion reaches a dynamic equilibrium.
- Plants use the ratio of the two forms to monitor and adapt to changes in light conditions.
  - If other trees shade a tree that requires high light intensity, its phytochrome ratio will shift in favor of P_r because the canopy screens out more red light than far-red light. The tree will allocate resources to growing taller.
  - If the target tree is in direct sunlight, the proportion of P_{fr} will increase, stimulating branching and inhibiting vertical growth.

Biological clocks control circadian rhythms in plants and other eukaryotes.

- Many plant processes, such as transpiration and synthesis of certain enzymes, undergo a daily oscillation.
- Even under constant conditions in a growth chamber, many physiological processes in plants, such as the opening and closing of stomata and the production of photosynthetic enzymes, continue to oscillate with a frequency of about 24 hours.
  - Many legumes lower their leaves in the evening and raise them in the morning, and these movements continue if the plants are kept in constant light or constant darkness.
- Physiological cycles with a frequency of about 24 hours that are not directly paced by any known environmental variable are called **circadian rhythms**.
- Because organisms continue their rhythms even when placed in mine shafts or orbited in satellites, the rhythms do not appear to be triggered by any subtle but pervasive environmental signal.
- All research thus far indicates that the clock for circadian rhythms is internal.
- This internal clock is set to a period of precisely 24 hours by daily signals from the environment.

- If an organism is kept in a constant environment, its circadian rhythms deviate from a 24-hour period to free-running periods ranging from 21 to 27 hours.
    - Deviations of the free-running period from 24 hours do not mean that the biological clocks drift erratically but that they are not synchronized with the outside world.
- In considering biological clocks, we need to distinguish between the clock and the rhythmic processes it controls.
    - If we restrain the leaves of a bean plant so that they cannot move, the leaves will return to the appropriate position for that time of day when we release them.
    - We can interfere with a biological rhythm, but the clockwork goes right on ticking off the time.
- Oscillations in the transcription of specific genes underlie circadian rhythms.
- 5% of the mRNAs transcribed by *Arabidopsis* undergo a circadian rhythm.
    - Some mRNAs are more abundant at dawn, others at dusk, and others at midday.
- The 24-hour period arises from negative feedback loops involving the transcription of a few central "clock genes."
    - Some clock genes may encode transcription factors that inhibit, after a time delay, the transcription of the gene that encodes the transcription factor itself.
    - These negative feedback loops, plus a time delay, are enough to produce oscillations.
- Researchers have recently used a novel technique to identify clock mutants in *Arabidopsis*.
    - Molecular biologists spliced the gene for luciferase (the enzyme responsible for bioluminescence in fireflies) to the promoter of certain photosynthesis-related genes that show circadian rhythms in transcription.
    - When the biological clock turned on the promoter of the photosynthesis genes in *Arabidopsis*, it also stimulated the production of luciferase, and the plant glowed.
    - This enabled researchers to screen plants for clock mutations, several of which are defects in proteins that normally bind photoreceptors.
    - These mutations may disrupt a light-dependent mechanism that sets the biological clock.

Light entrains the biological clock.

- Because the free-running period of many circadian rhythms is longer or shorter than the 24-hour daily cycle, the rhythms eventually become desynchronized with the natural environment when denied environmental cues.
    - Humans experience this type of desynchronization when we cross several times zones in an airplane, leading to the phenomenon called jet lag.
    - Eventually, our circadian rhythms become resynchronized with the external environment.
- Both phytochrome and blue-light photoreceptors can entrain the circadian rhythms of plants.
- The phytochrome system involves turning cellular responses off and on by means of the P_r ←→ P_{fr} switch.
    - In darkness, the phytochrome ratio shifts gradually in favor of the P_r form, in part from the synthesis of new P_r molecules and, in some species, by the slow biochemical conversion of P_{fr} to P_r.
    - When the sun rises, the P_{fr} level suddenly increases by rapid photoconversion of P_r.
    - This sudden increase in P_{fr} each day at dawn resets the biological clock.

- Interactions between phytochrome and the biological clock enable plants to measure the passage of night and day.
- The relative lengths of night and day change over the course of the year, except at the equator. Plants use this change to adjust their activities in synchrony with the seasons.

Photoperiodism synchronizes many plant responses to changes of season.

- The appropriate appearance of seasonal events, such as seed germination, flowering, and the onset and breaking of bud dormancy, is of critical importance in the life cycles of plants.
- The environmental stimulus that plants use most often to identify the time of year is the photoperiod, the relative lengths of night and day.
- A physiological response to the photoperiod, such as flowering, is called **photoperiodism**.
- One of the earliest clues to how plants detect the progress of the seasons came from a mutant variety of tobacco, Maryland Mammoth, that flowers only in winter.
- In light-regulated chambers, Maryland Mammoth flowered only if the day length was 14 hours or shorter, which explained why it did not flower during the longer days of the summer.
- Maryland Mammoth is a **short-day plant** that requires a light period *shorter* than a critical length to flower.
  - Other short-day plants are chrysanthemums, poinsettias, and some soybean varieties.
- **Long-day plants** flower only when the light period is *longer* than a critical number of hours.
  - Examples include spinach, radish, lettuce, iris, and many cereals.
- **Day-neutral plants** flower when they reach a certain stage of maturity, regardless of the day length.
  - Examples include tomatoes, rice, and dandelions.
- It is night length, not day length, which controls flowering and other responses to photoperiod.
  - Research found that cocklebur, a short-day plant, flowers if the light period is broken by a brief period of darkness, but not if the dark period is broken by a few minutes of dim light.
- Short-day plants are actually long-night plants, requiring a minimum length of uninterrupted darkness.
  - Cocklebur is unresponsive to day length, but requires at least 8 hours of continuous darkness to flower.
- Similarly, long-day plans are actually short-night plants.
  - A long-day plant grown with long nights that would not normally induce flowering will flower if the period of continuous darkness is interrupted by a few minutes of light.
- Although the critical factor is night length, the terms *long-day* and *short-day* are still used.
- Long-day and short-day plants are distinguished *not* by an absolute night length but by whether the critical night length sets a maximum (long-day plants) or minimum (short-day plants) number of hours of darkness required for flowering.
  - The actual number of hours in the critical night length is specific to each species of plant.
- Red light is the most effective color in interrupting the nighttime portion of the photoperiod.
- Action spectra and photoreversibility experiments show that phytochrome is the active pigment.

- If a flash of red light during the dark period is followed immediately by a flash of far-red light, the plant detects no interruption of night length, demonstrating red/far-red photoreversibility.
- Plants measure night length very accurately.
    - Some short-day plants won't flower if night is one minute shorter than the critical length.
    - Some plants species always flower on the same day each year.
- Humans can exploit the photoperiodic control of flowering.
    - By punctuating each long night with a flash of light, the floriculture industry can induce chrysanthemums, normally a short-day plant that blooms in fall, to delay their blooming until Mother's Day in May.
    - The plants interpret this time as not one long night but two short nights.
- Although some plants require only a single exposure to the appropriate photoperiod to begin flowering, others require several successive days of the appropriate photoperiod.
- Some plants respond to photoperiod only if exposed to another environmental stimulus.
    - Winter wheat will not flower unless it has been exposed to several weeks of temperatures below 10^0C (called **vernalization**) before exposure to the appropriate photoperiod.

Leaves detect photoperiod and trigger flowering.

- Although buds produce flowers, it is leaves that detect photoperiod and trigger flowering.
    - If even a single leaf receives the appropriate photoperiod, all buds on a plant can be induced to flower.
    - Plants that lack leaves will not flower even if exposed to the appropriate photoperiod.
- The flowering stimulus appears to be the same for short-day and long-day plants, despite differing photoperiod conditions required for leaves to send this signal.
- Large macromolecules, such as mRNA and proteins, can move symplastically via plasmodesmata and regulate plant development.
    - The flowering signal, called **florigen** appears to be such a macromolecule.
- A gene called *FLOWERING LOCUS T (FT)* is activated in leaf cells during conditions that favor flowering.
    - The FT protein travels to the shoot apical meristem and initiates flowering.
- Whatever combination of environmental cues (such as photoperiod or vernalization) and internal signals (such as the FT hormone) is necessary for flowering, the outcome is the transition of a bud's meristem from a vegetative state to a flowering state.
    - This requires that meristem identity genes that induce the bud to form a flower must be switched on.
    - Then organ identity genes that specify the spatial organization of floral organs—sepals, petals, stamens, and carpels—are activated in the appropriate regions of the meristem.

Concept 39.4 Plants respond to a wide variety of stimuli other than light

- Because plants are immobile, natural selection has created mechanisms that enable them to adjust to a wide range of environmental circumstances by developmental or physiological means.
- Many environmental stimuli influence plant development and physiology.

- The roots and shoots of plants respond to gravity by **gravitropism**.
- Roots demonstrate positive gravitropism and shoots exhibit negative gravitropism.
- Gravitropism ensures that the root grows into the soil and that the shoot reaches sunlight, regardless of how a seed is oriented when it lands.
- Plants detect gravity by the settling of **statoliths**, dense cytoplasmic components that settle under the influence of gravity to the lower portions of cells.
    - The statoliths of vascular plants are specialized plastids containing dense starch grains.
- In roots, statoliths are located in certain cells of the root cap.
    - In one hypothesis, the aggregation of statoliths at low points of these cells triggers a redistribution of calcium, which causes lateral transport of auxin within the root.
    - Calcium and auxin accumulate on the lower side of the zone of elongation, inhibiting cell elongation, slowing growth on that side, and curving the root downward.
- Experiments with *Arabidopsis* and tobacco mutants lacking statoliths are still capable of gravitropism but have a slower response than wild-type plants.
    - Perhaps the entire cell helps the root sense gravity by mechanically pulling on proteins that tether the protoplast to the cell wall, stretching proteins on the "up" side and compressing proteins on the "down" side.
    - Other dense organelles also contribute to gravitropism by distorting the cytoskeleton.
    - Statoliths, because of their density, may enhance gravitational sensing.
- Plants change form with mechanical perturbations, a response called **thigmomorphogenesis**.
    - Thigmomorphogenesis may be seen by comparing a short, stocky tree growing on a windy mountain ridge with a taller, more slender member of the same species growing in a more sheltered location.
- Plants are sensitive to mechanical stress: Measuring the length of a leaf with a ruler alters its subsequent growth.
    - Rubbing the stem of a young plant results in plants that are shorter than controls.
- Some plant species have become, over the course of their evolution, "touch specialists."
    - Vines and other climbing plants have tendrils that coil around supports.
    - Contact stimulates a coiling response caused by the differential growth of cells on opposite sides of the tendril.
- Directional growth in response to touch is **thigmotropism**, which allows a vine to take advantage of whatever mechanical support it comes across as it climbs upward toward a forest canopy.
- Some touch specialists undergo rapid leaf movements in response to mechanical stimulation.
- When the compound leaf of the sensitive plant *Mimosa pudica* is touched, it collapses and leaflets fold together.
    - This occurs when pulvini, specialized motor organs at the joints of leaves, become flaccid from a loss of K^+ and subsequent loss of water by osmosis.
    - It takes 10 minutes for the cells to regain their turgor.
- The folding of *Mimosa* leaves may reduce surface area, reducing water loss, or expose thorns on the stem, deterring herbivory.
- One remarkable feature of rapid leaf movement is that signals are transmitted from leaflet to leaflet via **action potentials**.

- Traveling at about a centimeter per second through the leaf, these electrical impulses resemble nervous system messages in animals, although they are much slower.

- Action potentials, which have been discovered in many species of algae and plants, may be widely used as a form of internal communication.
  - In the carnivorous Venus' flytrap *(Dionaea muscipula)*, stimulation of sensory hairs in the trap results in an action potential that travels to the cells that close the trap.

Plants may face environmental stress.

- Occasionally, factors in the environment change severely enough to have an adverse effect on a plant's survival, growth, and reproduction.
  - Environmental stresses such as flooding, drought, or extreme temperatures can devastate crop yields.
  - In natural ecosystems, plants that cannot tolerate environmental stress either succumb or are outcompeted by other plants, and they may become locally extinct.
- Environmental stresses, both **biotic** and **abiotic**, are important in determining the geographic range of plants.
- On a sunny, dry day, a plant may wilt because it is losing water by transpiration faster than water can be restored by uptake from the soil.
  - Prolonged drought can stress or even kill crops and plants in natural ecosystems.
  - Plants have control systems that enable them to cope with less extreme water deficits.
- Much of the plant's response to a water deficit helps the plant conserve water by reducing the rate of transpiration.
- Water deficit in a leaf causes guard cells to lose turgor and the stomata close.
  - A water deficit also stimulates increased synthesis and release of abscisic acid in a leaf, which signals guard cells to close stomata and minimizes transpirational water loss.
- As leaves of grasses wilt, they roll into a shape that reduces transpiration by exposing less leaf surface to dry air and wind.
  - Other plants shed leaves in response to seasonal drought. This reduces photosynthesis.
- Root growth also responds to water deficit.
  - During a drought, soil dries from the surface down.
  - This inhibits the growth of shallow roots, partly because cells cannot maintain the turgor required for elongation.
- Deeper roots surrounded by soil that is still moist continue to grow, and the root system proliferates in a way that maximizes exposure to soil water.
- Plants in flooded soils (or overwatered houseplants) may suffocate because the soil lacks the air spaces that provide oxygen for cellular respiration in the roots.
- Some plants are structurally adapted to very wet habitats.
  - Mangroves, inhabitants of coastal marshes, have aerial roots with access to oxygen.
  - Less specialized plants in waterlogged soils produce ethylene in the roots, causing some cortical cells to undergo apoptosis and creating air tubes that function as "snorkels."
- An excess of sodium chloride or other salts in the soil threaten plants for two reasons.
  1. By lowering the water potential of the soil solution, salt can cause a water deficit in plants even though the soil has plenty of water.

- As the water potential of the soil solution becomes more negative, the water potential gradient from soil to roots is lowered, thereby reducing water uptake.

2. Sodium and certain other ions are toxic to plants at concentrations high enough to overwhelm the selective permeability capabilities of root cell membranes.

- Many plants produce organic compounds that keep the water potential of the cell more negative than that of the soil, without admitting toxic quantities of salt.
- Most plants cannot survive salt stress for long. The exceptions are halophytes, salt-tolerant plants with adaptations such as salt glands that pump salts out across the leaf epidermis.
- Excessive heat can harm or kill a plant by denaturing its enzymes and disrupting its metabolism.
  - Transpiration helps dissipate excess heat through evaporative cooling, but it may cause a water deficit.
  - Closing stomata to preserve water sacrifices evaporative cooling.
- Most plants have a backup response that enables them to survive heat stress.
  - Above a certain temperature—about 40^0C for most plants in temperate regions—plant cells begin to synthesize **heat-shock proteins** to protect other proteins from heat stress.
  - Some heat-shock proteins are chaperone proteins, which function in unstressed cells as temporary scaffolds that help other proteins fold into their functional shapes.
  - Heat-shock proteins bind to other proteins and help prevent their denaturation.
- One problem that plants face when the temperature of the environment falls is a change in the fluidity of cell membranes.
  - When the temperature becomes too cool, lipids are locked into crystalline structures and membranes lose their fluidity, which adversely affects solute transport and the functions of other membrane proteins.
- One solution is to alter the lipid composition in the membranes, increasing the proportion of unsaturated fatty acids, which have shapes that keep membranes fluid at lower temperatures by impeding crystal formation.
  - This response requires several hours to days, which is one reason rapid chilling is generally more stressful than gradual seasonal cooling.
- Freezing is another type of cold stress.
  - At subfreezing temperatures, ice forms in cell walls and intercellular spaces.
  - Solutes in the cytosol depress its freezing point, lowering extracellular water potential, and causing water to leave the cytoplasm.
  - The resulting increase in the concentration of salt ions in the cytoplasm is harmful and can lead to cell death.
- Plants native to regions where winters are cold have special adaptations that enable them to cope with freezing stress.
  - The cells of many frost-tolerant species have higher cytoplasmic levels of specific solutes, such as sugars, that are well tolerated at high concentrations and help reduce water loss from the cell during extracellular freezing.
  - The unsaturation of membrane lipids also increases, thereby maintaining proper levels of membrane fluidity.
- Some plants have special *antifreeze proteins* that hinder ice crystals from growing, making it possible to escape freezing damage.

- Antifreeze proteins bind to small ice crystals and inhibit their growth or prevent the recrystallization of ice.

- Five major classes of antifreeze proteins differ markedly in their amino acid sequences but have a similar three-dimensional structure, suggesting convergent evolution.
  - Antifreeze proteins from winter rye are homologous to antifungal proteins called PR proteins, but they are produced in response to cold temperatures and shorter days, not fungal pathogens.
- Progress is being made in increasing the freezing tolerance of crop plants by genetically engineering antifreeze protein genes into their genomes.

Concept 39.5 Plants respond to attacks by herbivores and pathogens

- Plants interact with many other species in their communities.
- Some of these interspecies interactions are mutually beneficial, such as associations with fungi in mycorrhizae or with insect pollinators.
- Most interspecies interactions do not benefit the plant.
  - As primary producers, plants are at the base of most food webs and are subject to attack by a wide variety of herbivores.
  - Plants are also subject to attacks by pathogenic viruses, bacteria, and fungi.
- Plants counter these threats with defense systems that deter herbivory and prevent infection or combat pathogens that infect the plant.

Plants deter herbivores with both physical and chemical defenses.

- Herbivory—animals eating plants—is a stress for plants in any ecosystem.
- Plants resist herbivory with both physical defenses, such as thorns and trichomes, and chemical defenses, such as the production of distasteful or toxic compounds.
- Some plants produce an unusual amino acid, *canavanine,* which resembles arginine.
  - If an insect eats a plant containing canavanine, the molecule is incorporated into the insect's proteins in place of arginine.
  - Because canavanine is different enough from arginine to adversely affect the conformation and function of proteins, the insect dies.
- Some plants "recruit" predatory animals that help defend them against specific herbivores.
  - A leaf damaged by caterpillars releases volatile compounds that attract parasitoid wasps.
  - Parasitoid wasps inject their eggs into their caterpillar prey.
  - The eggs hatch within the caterpillars, and the larvae eat through their organic containers from the inside out.
  - The stimulus for the leaf's response is a combination of physical damage to the leaf caused by the munching caterpillar and a specific compound in the caterpillar's saliva.
- These volatile molecules can also function as an "early warning system" for nearby plants of the same species.
  - Lima bean plants infested with spider mites release volatile chemicals that signal the attack to neighboring, noninfested lima bean plants.
  - The neighbors respond with release of volatiles that attract predatory mites.

- Researchers transgenically engineered *Arabidopsis* plants to produce two volatile chemicals that have been found to attract carnivorous predatory mites in other plants.
- Predatory mites were attracted to the genetically modified *Arabidopsis*, a finding with implications for the genetic engineering of insect resistance in crop plants.

Plants use multiple lines of defense against pathogens.

- A plant's first line of defense against infection is the physical barrier of the epidermis of the primary plant body and the periderm of the secondary plant body.
- Mechanical wounding of leaves by herbivores may allow pathogen invasion.
    - Viruses, bacteria, and the spores and hyphae of fungi can enter the plant through injuries or through natural openings in the epidermis, such as stomata.
- After a pathogen invades, the plant mounts a chemical attack as a second line of defense that destroys the pathogens and prevents their spread from the site of infection.
- Plants can recognize certain invading pathogens. Successful pathogens cause disease because they are able to evade recognition or suppress host defense mechanisms.
    - Those pathogens against which a plant has little specific defense are said to be **virulent**.
    - **Avirulent** pathogens gain access to their host without severely damaging the plant.
- **Gene-for-gene recognition** is a widespread form of plant disease resistance that involves the recognition of molecules called *elicitors* by the proteins produced by plant disease resistance *(R)* genes.
    - There are many pathogens, and plants have many *R* genes; *Arabidopsis* has several hundred.
- An R protein usually recognizes only a single corresponding pathogen molecule that is encoded by an avirulence *(Avr)* gene.
- Avr proteins are harmful to the plant, redirecting host metabolism to the advantage of the pathogen.
- The recognition of elicitors by R proteins triggers signal transduction pathways that lead to the activation of defense responses, including a localized hypersensitive response and **systemic acquired resistance**.
- Local and systemic responses to pathogens require extensive genetic reprogramming and commitment of cellular resources.
- Plants activate their defenses only after they detect an invading pathogen.
- The hypersensitive response (HR) is a complex early defense response that causes cell and tissue death near the infection site and restricts the spread of a pathogen.
    - After cells at the infection site mount a chemical defense and seal off the area, they destroy themselves.
- The HR is initiated when pathogen elicitors bind to R proteins, altering the selective permeability of the plasma membrane and stimulating the production of *phytoalexins*, toxic compounds with fungicidal and bactericidal properties.
    - The HR also induces the production of *PR proteins* (pathogenesis-related proteins), which hydrolyze components in the cell walls of the pathogens.
    - Infection also stimulates the formation of lignin and the cross-linking of molecules in the plant cell wall, hindering the spread of the pathogen to other parts of the plant.

- Pathogen invasions can also produce chemical signals that “sound the alarm” of infection to the whole plant.
- The resulting **systemic acquired resistance** (SAR), associated with the systemic expression of some defense genes, is nonspecific, providing protection against many pathogens for days.
- Methylsalicylic acid is produced around the infection site and carried by phloem throughout the plant, where it is converted to **salicylic acid** in areas remote from the site of infection.
    - Salicylic acid activates a signal transduction pathway that induces the production of PR proteins and resistance to pathogen attack.